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HOME-RANGE SIZE, RESPONSE TO FIRE, AND HABITAT PREFERENCES OF WINTERING HENSLOW'S SPARROWS

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ABSTRACT.—Henslow's Sparrow (*Ammodramus henslowii*) is a declining, disturbance-dependent grassland bird that winters in the longleaf pine (*Pinus palustris*) ecosystem of the southeastern United States. During two winters (2001, 2002), we estimated the relative abundances, movement patterns, and habitat associations of Henslow's Sparrows wintering in habitat patches differing in time since last burn (burn treatment). We conducted our study in southeastern Louisiana in *Andropogon* spp.-dominated longleaf pine savanna habitat. Henslow's Sparrows were most abundant in savannas burned the previous growing season, with a mean relative abundance of 2.6 individuals/ha. The most dramatic decline occurred between burn year 0 and year 1 (first and second winters after burning), when mean relative abundance dropped to 1.0 individual/ha. Home-range size of radio-tagged birds was not correlated with burn treatment. All radio-tagged individuals maintained stable home ranges, with a mean size of 0.30 ha. Vegetation characteristics differed significantly among burn treatments. Sites burned the previous growing season had low vegetation density near the ground, vegetation taller than 1.0 m, and high seed abundance. These variables were all highly correlated with Henslow's Sparrow relative abundance, but seed density best predicted Henslow's Sparrow numbers. We recommend a biennial, rotational burn regime to maintain habitat characteristics correlated with Henslow's Sparrow abundance. *Received 8 November 2004, accepted 11 June 2005.*

The Henslow's Sparrow (*Ammodramus henslowii*) is one of the fastest-declining disturbance-dependent bird species in North America. Breeding populations, which range from southern Canada through the Northeast and Midwest of the United States, have been decreasing at a rate of 8.6% per year since 1966 (Sauer et al. 2004), likely due to habitat loss (Askins 1993, Pruitt 1996, Herkert 1997, Cully and Michaels 2000). Breeding habitat requirements are generally well understood. Henslow's Sparrows respond favorably to burning, haying, mowing, and hardwood reduction, achieving highest breeding densities 2–4 years after disturbance, when herbaceous vegetation is dense and woody vegetation is sparse (Zimmerman 1988; Herkert 1991, 1994, 1998; Swengel 1996; Herkert and Glass 1999; Cully and Michaels 2000).

Secretive winter behavior prevents an accurate regional estimation of winter population status, but there is some information on habitat use patterns. Henslow's Sparrows winter along the southeastern Gulf Coastal Plain, a region historically dominated by the fire-maintained longleaf pine (*Pinus palustris*) ecosystem. Studies in Mississippi (Chandler and Woodrey 1995), western Louisiana (Carrie et al. 2002), and along the Florida-Alabama border (Plentovich et al. 1999, Tucker and Robinson 2003) have revealed greater winter abundance of Henslow's Sparrows in

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recently burned or disturbed sites; furthermore, there is evidence that Henslow's Sparrows exhibit site fidelity over the winter, although no between-year recaptures have been documented (Plentovich et al. 1998). Home-range size during winter has not been estimated. Two studies have included banding wintering Henslow's Sparrows, but neither study has attempted to systematically estimate abundance using capture data (Chandler and Woodrey 1995, Plentovich et al. 1998).

Wintering Henslow's Sparrows have been associated with a variety of habitat characteristics, partially because each study conducted so far has considered a different community within the longleaf pine ecosystem. Habitat associations have been studied in lowland pitcher plant bogs, clearcut pine plantations, and upland savannas managed for timber production (Plentovich et al. 1998, 1999; Carrie et al. 2002; Tucker and Robinson 2003). Henslow's Sparrow presence and abundance have been correlated with the density of *Panicum verrucosum* and *Sarracenia* spp. (Plentovich et al. 1999), low litter depth and a high percent cover of herbaceous vegetation (Carrie et al. 2002), and high seed abundance and forb density (Tucker and Robinson 2003). No study has included dominant grass species composition among the vegetation measurements. Also, no study has emphasized winter habitat use of Henslow's Sparrows on upland longleaf pine savannas managed to restore the floristics of the savannas that historically dominated the southeastern Gulf Coastal Plain.

The longleaf pine ecosystem, including upland savanna communities, once dominated 25–36 million ha of the southeastern United States (Platt et al. 1988, Frost 1993, Stout and Marion 1993, Ware et al. 1993). Historically, fires occurred approximately every 1–3 years, usually during the summer (Frost et al. 1986, Stout and Marion 1993, Frost 1998). Longleaf pine savanna has a bi-layered habitat structure. Sparse stands of fire-tolerant longleaf pines form the overstory and a diverse herbaceous community occupies the understory. Without frequent fires, this ecosystem develops into a beech-magnolia-sweet gum forest (Ware et al. 1993).

In the Southeast, more than 98% of the original longleaf pine ecosystem has been lost (Frost 1993, Ware et al. 1993, Noss et al. 1995). In Louisiana, 95–99% of this habitat has been destroyed (Noss et al. 1995). The remaining habitat consists of remnants scattered across the landscape, and it is estimated that less than 0.7% (280,000 ha) of that is in good, fire-managed condition (Frost 1993).

Considering the population declines and habitat loss experienced by Henslow's Sparrows, effective habitat management is vital. To assess the effects of prescribed burning on wintering Henlsow's Sparrows in southeastern Louisiana, we intensively monitored savanna remnants managed under differing fire-return intervals. We used capture data to estimate relative abundance and radio-transmitters to provide the first estimates of home-range size for wintering Henslow's Sparrows; we report the first between-year recaptures of wintering individuals. We also conducted comprehensive measurements of habitat characteristics, including vegetation structure, species composition of grasses, and seed abundance. Finally, we discuss our results and make management recommendations based on our results and those of previous studies.

METHODS

Study sites.—We chose eight study sites (see Table 1 for site names) located in St. Tammany and Tangipahoa parishes of southeastern Louisiana. This region lies on the boundary of the Coastal Plain Rolling Hills and Coastal Flatlands, historically dominated by longleaf pine/*Andropogon* spp. savanna (Frost 1993, Peet and Allard 1993). Study sites were dominated by native vegetation and were located within larger management areas composed of savanna and mixed woodlands. Site selection was based on amount of contiguous savanna (>15 ha) and relative cover of woody vegetation. We required study sites with <30% shrub cover so as not to impede mist-net sampling (see below).

At the time of the study, all sites had been fire-managed for at least 4 years, under the responsibility of The Nature Conservancy of Louisiana, the Louisiana Department of Wildlife and Fisheries, or the Girl Scouts of America. Study sites (areas sampled) were 2.25–7.5 ha; most were ≥6.25 ha (Table 1). Total savanna area surrounding each site differed. Study sites within the same burn regime were

TABLE 1. Burn treatments and recent fire history of eight study sites in longleaf pine savanna sampled during winters 2001 and 2002, in Tangipahoa and St. Tammany parishes, southeastern Louisiana.

Site name	Management area (size in ha)	Years since burn 2001	Years since burn 2002	Burn season and year	Area sampled 2001 (ha)	Area sampled 2002 (ha)
RAM	Lake Ramsay Wildlife Management Area (489.7)	Not sampled	0	Summer 2001[a]	—	5.18
GSC	Camp Whispering Pines (19.0)	Not sampled	0	May 2001	—	2.25
BU1	Abita Creek Flatwoods Preserve (321.3)	0	1	May 2000	4.76	6.13
BU3	Abita Creek Flatwoods Preserve (321.3)	0	1	May 2000	7.03	6.69
LRS	Lake Ramsay Wildlife Management Area (489.7)	1	2	May 1999	6.25	6.25
LRN	Lake Ramsay Wildlife Management Area (489.7)	1	2	May 1999	6.25	6.25
TNC	Lake Ramsay Wildlife Management Area (489.7)	2	3	July 1998	7.50	6.25
WMA	Lake Ramsay Wildlife Management Area (489.7)	2	3	August 1998	6.25	6.25

[a] Exact date unavailable from management area records.

separated by ≥0.63 km. In 2001, we monitored six sites, comprising two replicates each of three burn regimes (burn treatments): 0, 1, and 2 years since last burn. Year-0 sites were burned the growing season prior to sampling; for example, a site burned in May 2000 was sampled in January 2001. In 2002, we followed these six sites as they transitioned into the next burn treatment level and added two replicates in the year-0 burn treatment (Table 1).

Relative abundance sampling.—Relative abundance estimates of Henslow's Sparrows were based on systematic mist-net sampling of each study site. Sampling took place during two consecutive winter seasons: January through February 2001 (winter 2001) and late November 2001 through February 2002 (winter 2002). During winter 2001, we sampled each site twice, once in January and once in February. During winter 2002, each site was sampled four times: we repeated the January and February (2001) sampling protocol at each study site, and we took two more samples of a 2.25-ha subset within each site. Subsets were chosen consistently across all study sites to measure 150 m on a side, starting at the most accessible corner of the 6.25-ha plot. We deviated from this protocol at three sites in 2002 because of limited volunteers, inclement weather, and unscheduled burn events. At site GSC, we conducted three 2.25-ha samples. We sampled site TNC three times—two 6.25-ha samples and one 2.25-ha sample. WMA was sampled twice—one 2.25-ha sample and one 5.0-ha sample. Overall, we completed 40 sampling events on our eight study sites over the two study seasons.

For mist-net sampling, we used a team of 4–10 people, spaced 3 m apart, moving systematically across the study site (M. S. Woodrey pers. comm.). The team maintained their spacing throughout the sampling event to ensure even coverage of the site. Each time an *Ammodramus* sparrow flushed, the team marked the spot where they were walking, marked the area where the sparrow emerged from the herbaceous layer ("flush-from" location), and quickly set up a 6.0 × 2.5-m mist net near where the sparrow landed (capture location). The team then attempted to flush the sparrow into the net. All captured individuals were banded with a federal band (size 0A). A subset of Henlsow's Sparrows was fitted with radio-transmitters (see *Henslow's Sparrow movement patterns* below). Birds with radio-transmitters were released at their "flush-from" location and birds without radio-transmitters were released at their capture location.

Relative abundance analysis.—Based on their similar behavior as they flushed from the grass, we also pursued Le Conte's Sparrows

(*Ammodramus leconteii*), which often could be distinguished from Henslow's Sparrows only after being flushed into the net. During some sampling events, we detected one or more *Ammodramus* sparrows that we were unable to capture or otherwise identify to species level. To estimate the relative abundance of each species across our study sites, we assumed that the relative proportion of identified *Ammodramus* sparrows reflected the real relative abundance of each species. For each sampling event, we assigned unidentified *Ammodramus* individuals to either Henslow's or Le Conte's based on the abundance of identified *Ammodramus* sparrows during that sampling event. In 2001, we had to adjust 75% of the samples; in 2002, when Le Conte's Sparrow abundance was much lower, this adjustment was seldom needed (28% of samples adjusted).

We estimated relative abundance (Henslow's Sparrows/ha) by dividing the number of birds detected during a sampling event by the area sampled during that event. We used a nested analysis of variance (ANOVA) model to evaluate differences in relative abundance across burn treatments and study sites. Time since burn (burn treatment) was the main effect, site was nested within burn treatment, and sampling event was the sampling unit. Since previous studies have revealed that more recently burned sites should have a greater abundance of Henslow's Sparrows, we used an *a priori* contrast to compare Henslow's Sparrow abundance in burn treatment year 0 with all other burn treatments. We also evaluated whether sampling-team size was related to abundance estimates by regressing rank transformed Henslow's Sparrow abundance for the 40 sampling events on sampling-team size.

Henslow's Sparrow movement patterns.—A subset of birds ($n = 27$) captured during sampling events of winters 2001 and 2002 were fitted with radio-transmitters to determine movement patterns. We followed two or three individuals on each replicate of burn treatments 0 and 1 in 2001 and on burn treatments 0, 1, and 2 in 2002 ($n = 5$ sites). Transmitters (model BD-2A; Holohil Systems, Carp, Ontario, Canada) weighing 0.70 g (5.38% of mean body weight) were attached with elastic leg-loop harnesses (Rappole and Tipton 1991). Projected battery life was 21 days. Individuals were located daily by triangulation using a three-element yagi antenna and a Wildlife Materials TRX-64S (Murphysboro, Illinois) receiver. A single observer conducted all triangulations used in analyses. Locations consisted of 2–3 bearings to minimize time between triangulations (mean = 2.4 bearings). Mean time between triangulations was 5.9 min (SE = 0.53). Individuals were rarely seen, and triangulations were made from at least 12 m (mean = 41.4 m, SE = 2.98) away to minimize observer effects on the behavior of radio-tagged birds.

Telemetry data analysis.—Home-range estimates were based on 9 to 26 locations per individual (mean = 15.9, SE = 0.96). We used the program Location of a Signal (Ecological Software Solutions 2000) to compute locations from compass bearing data. Locations were entered into ArcView (ESRI, Inc. 1999) as Cartesian coordinates and we used the Animal Movement extension (Hooge and Eichenlaub 1997) to determine home-range size. We used a bootstrap ($n = 100$, interval = 1, with replacement) of the minimum convex polygon estimate of 11 locations ($n = 16$ individuals) to determine mean home-range size. The bootstrap of nine locations ($n = 18$ individuals) was used to analyze home-range size differences across burn treatments, study sites, and study years using ANOVA. Home-range size estimates were natural-log transformed to meet assumptions of normality and homogeneity of variances.

We examined the bootstrapped minimum convex polygon home-range estimates available for each individual to decide how many locations to include in the analyses described above. After nine locations (the minimum for any individual), the empirical mean home-range size reached 74% (SE = 0.03) of the bootstrapped estimate. With 11 locations, the empirical mean reached 83% (SE = 0.03) of the bootstrapped estimate. Based on these results, our mean estimate of home-range size probably represents at least 83% of the actual home range for all of our individuals, with more accurate estimates for most individuals. Home-range size for wintering Henslow's Sparrows stabilized at an average of 21 locations during a study at the Mississippi Sandhill Crane National Wildlife Refuge (Thatcher

TABLE 2. Dominant grass species encountered on longleaf pine savanna study sites in southeastern Louisiana during winters 2001 and 2002, grouped by morphotypes used in analyses.

Dominant grass morphotypes	Species included
Andropogon spp./*Schizachyrium scoparium*	*Andropogon mohrii, A. virginicus, A. gerardii, Schizachyrium scoparium*
Panicum virgatum/P. rigidulum	*Panicum virgatum, P. rigidulum*
Dichanthelium scabriusculum, Schizachyrium tenerum	*Dichanthelium scabriusculum, Schizachyrium tenerum*
Muhlenbergia expansa	*Muhlenbergia expansa* (with mature inflorescences)
Muhlenbergia expansa (without mature inflorescences)	*Muhlenbergia expansa* (without mature inflorescences)
Ctenium aromaticum	*Ctenium aromaticum*
Aristida spp.	*Aristida purpurascens, A. dichotoma, A. affinis, A. palustris*
Dichanthelium spp.	*Dichanthelium longiligulatum, D. acuminatum, D. dichotomum*

2003), suggesting that our estimates were probably close to stabilizing for most birds.

We used regression analysis to look for relationships between the relative abundance and mean home-range size of Henslow's Sparrows at each site (bootstrap of nine locations, $n = 21$ individuals). Mean relative abundance at each study site was determined by summing the number of Henslow's Sparrows/ha detected during each sampling event and dividing that number by the total number of sampling events at that site.

Characterizing vegetation.—During the two winter study seasons, we randomly chose ten 10-m-radius plots within each study site and sampled vegetation structure, dominant grass species composition, and seed abundance. The aggregate of plots covered 5% of the area at each study site. Only five vegetation plots were sampled at one study site (GSC), which was only 2.25 ha in area. The same observer conducted all vegetation sampling, always during February to early March, before the onset of spring growth.

We measured vegetation structure as vegetation height, type of tallest vegetation, and density (using a 2.0-m pole marked in 10-cm increments). We measured 21 points in each vegetation plot: the center point and 5 measurements (every 2 m) in each of the four cardinal directions (M. S. Woodrey pers. comm.). Vegetation height was measured as the tallest vegetation to fall within a 30-cm radius of the vegetation pole. We classified type of tallest vegetation as herbaceous or woody. Vegetation density was measured at 9 of the 21 points within each vegetation plot. We counted the number of vegetative contacts with the pole within each 10-cm increment to estimate density. Number of contacts ranged from 0 to 10; contact counts >10 were placed in the "ten" category. Percent cover of woody vegetation was measured by visually estimating (to the nearest 5%) shrub cover and by counting the number of trees >7.5 cm dbh within the plot.

In each plot, we visually estimated percent cover of dominant grass species to the nearest 5%. All herbaceous cover visible from above was included, so totals could be greater than 100% if a sparse layer of grasses or shrubs revealed an understory. In our estimates of percent cover, we grouped some species together if they had similar growth habits (Table 2). We separated one species, *Muhlenbergia expansa*, into plants with and without mature inflorescences. The mature inflorescences of *Muhlenbergia expansa* did not persist past the first winter, allowing us to readily distinguish plants that had flowered the previous growing season from those that had not.

We estimated relative seed abundance by counting the number of stalks with mature inflorescences within one randomly placed 1.0-m^2 frame in each vegetation plot. Stalks were identified to genus or to species level when possible. We removed the grasses *Dichanthelium* spp. and *Schizachyrium tenerum* from the seed abundance analysis because of the difficulty in distinguishing senescent stalks from seed-producing stalks of the season. We excluded one site (LRS 2001) in seed abundance analyses because stalks with mature inflorescences were not identified to species during data collection.

Vegetation analysis.—Due to an unscheduled burn of one site, we collected vegetation data at only one site in the 3-year treatment. Therefore, we included only sites in the 0-, 1-, and 2-year treatments in the vegetation analysis, yielding four replicates of these three treatments over the study period.

We used two principal components analyses (PCA) with varimax rotation to describe vegetation structure and species composition of grasses across burn treatments and study sites. The PCA describing vegetation structure included vegetation height, vegetation density at heights from 0 to 0.3 m, percent shrub cover, number of woody contacts, and number of trees. We included vegetation density only from 0 to 0.3 m because a preliminary ANOVA showed that vegetation density at heights above 0.3 m did not differ among burn treatments. The PCA describing species composition included the percent cover values for the nine dominant grass species. Variables that loaded across more than one axis, or that did not load on any axis, were removed from the PCAs and treated separately.

PCA scores for structure and species composition were rank-transformed to meet assumptions for parametric tests, and a nested ANOVA model was used to test for differences in vegetation characteristics among burn treatments and among sites within burn treatments. Burn treatment was the main effect, sites were nested within burn treatment, and vegetation plot was the sampling unit. When tests were significant, we used Bonferroni multiple comparisons to compare variation among individual treatments (Sokal and Rohlf 1995). Percent cover values of dominant grass species that did not load in the principle components analysis were rank-transformed and included in the backwards-stepwise multiple linear regression analysis described below. We used SYSTAT (SPSS, Inc. 2000) for all analyses. Data points were considered outliers and removed from analysis if Student *t*-values were >3.0.

Seed abundance estimates were square-root transformed to meet assumptions of normality and homoscedasticity. We used a nested ANOVA model to examine differences in seed abundance across burn treatments and sites within treatments. We used a Bonferroni multiple comparison to examine relative differences among burn treatments.

We used backwards-stepwise multiple linear regression analysis to examine the relationship of vegetation characteristics to Henslow's Sparrow abundance. Variables were eliminated from analysis if they did not explain a significant amount of variation in Henslow's Sparrow abundance ($P > 0.05$) or if they were highly collinear (tolerance > 0.10).

RESULTS

Abundance in relation to burn treatment.—We detected 226 *Ammodramus* sparrows on the study sites over both years: 100 in 2001 and 126 in 2002. Identified birds included 135 Henslow's Sparrows, 23 LeConte's Sparrows, and 1 Grasshopper Sparrow (*Ammodramus savannarum*) during 40 sampling events. Of these, 88 Henslow's Sparrows were banded. Henslow's Sparrow abundance averaged 1.17 ± 0.32 individuals/ha, but was highly variable among study sites, ranging from 0 to 4.50 individuals/ha.

Henslow's Sparrow relative abundance was highest in the most recently burned sites (ANOVA, $F_{3,10} = 3.61$, $P = 0.053$; *a priori* contrast 0 [mean = 2.61 ± 0.40] versus all other burn treatments [mean = 0.75 ± 0.14], $F_{1,10} = 10.49$, $P = 0.009$; Fig. 1). Henslow's Sparrow abundance did not vary significantly between study years (winter 2001: mean = 0.84 ± 0.21; winter 2002: mean = 1.45 ± 0.26; ANOVA, $F_{1,38} = 2.05$, $P = 0.16$), but did vary across study sites within burn treatments 0 and 2 (ANOVA, burn treatment 0: $F_{3,7} = 19.74$, $P = 0.001$; burn treatment 1: $F_{3,8} = 1.39$, $P = 0.32$; burn treatment 2: $F_{3,8} = 15.22$, $P = 0.001$; burn treatment 3: $F_{1,3} = 1.80$, $P = 0.27$). Mean sampling-team size was 6.6 ± 0.23 people. Sampling-team size was evenly distributed across burn treatments and showed no relationship to the number of Henslow's Sparrows detected/ha ($F_{1,38} = 0.64$, $P = 0.43$, $R^2 = 0.02$).

Home-range size and site fidelity.—We banded 32 Henslow's Sparrows in 2001. Among the 58 individuals captured in 2002, 2 were recaptures from 2001. Both recaptures were found within the management area of

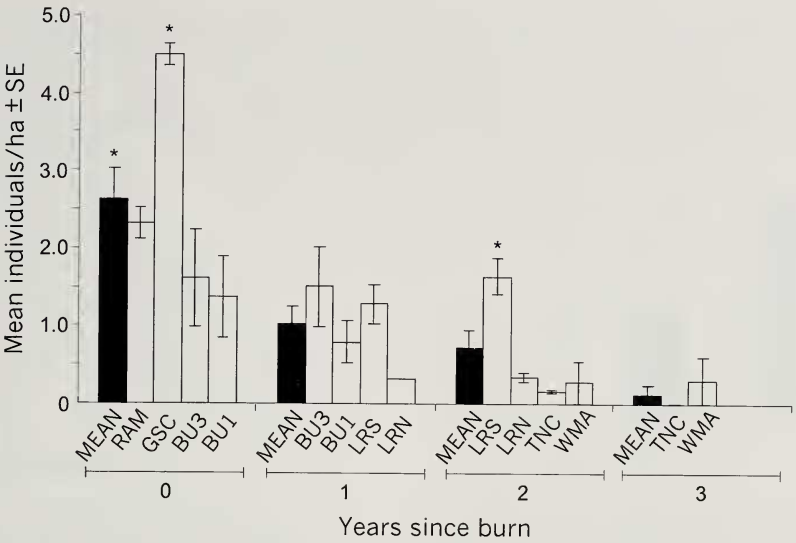

FIG. 1. In southeastern Louisiana during winters 2001 and 2002, Henslow's Sparrow abundance was greatest in longleaf pine savanna study sites the first winter after a burn, as revealed by a nested ANOVA and an *a priori* contrast of burn treatment 0 (i.e., 0 years since last burn) versus all other burn treatments (filled bars, significant difference indicated by asterisk). Mean abundance of Henslow's Sparrows varied within some burn treatments, but the overall pattern of decreasing abundance with increasing time since burn is apparent (unfilled bars). Asterisks over unfilled bars indicate significant differences within burn treatments, as revealed by one-way ANOVAs.

original capture; one was found on a different study site 1.6 km away (LRS burn treatment 1 to RAM burn treatment 0), and the other was found on the same study site (LRS burn treatment 1 to LRS burn treatment 2). We recaptured eight individuals within study years. Recaptures occurred in all burn treatments except year 3 and were always on the site of initial capture. The mean time between first and last capture was 42 days. Maximum time between captures was 70 days.

We radio-tagged 27 individuals at five study sites during winters 2001 and 2002. Of these, 21 individuals wore their radios long enough to allow estimation of home-range size (n = 9 locations). Three individuals at LRN in 2001 were not included in calculations of mean home-range size or in analyses. Home-range sizes at LRN in 2001 ranged from 0.92 to 3.31 ha (n = 3 individuals using 11 locations). These individuals were the only individuals monitored by a second observer and were outliers in all analyses. Including these outliers disproportionately influenced the mean home-range size estimate, but did not change the results of nonparametric tests of the analyses described below.

Home-range size varied from 0.09 to 1.50 ha (n = 16 individuals using 11 locations). All radio-tagged individuals maintained stable home ranges over the sampling period. Mean home-range size for Henslow's Sparrows wintering on our study sites was 0.30 ha (SE = 0.09, n = 16 individuals using 11 locations). Home-range size did not vary across study years ($F_{1,16} = 0.30$, $P = 0.59$) or sites ($F_{4,13} = 0.97$, $P = 0.46$; Fig. 2). There was no difference in home-range size across burn treatments ($F_{2,15} = 0.52$, $P = 0.61$). Home-range size was not related to relative abundance determined from mist netting ($F_{1,6} = 2.13$, $P = 0.20$, $R^2 = 0.26$).

Vegetation structure.—The PCA of vegetation structure revealed two factors that explained 68.8% of the variation in the data. Mean density between 0 and 0.3 m and mean height were inversely related on principal components axis 1 (HEIGHT/DENSITY) and explained 43.0% of the variation. Number of trees, percent shrub cover, and number of woody contacts loaded positively on principle components axis 2 (WOODY) and explained 25.8% of the variation in the data. HEIGHT/DENSITY varied significantly among burn treat-

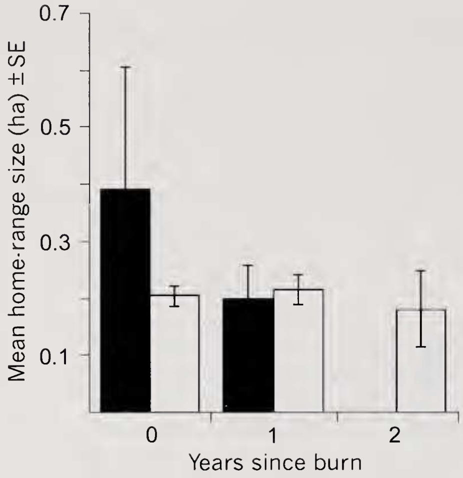

FIG. 2. Mean home-range size for Henslow's Sparrows ($n = 18$ individuals, 9 locations) wintering in longleaf pine savannas of southeastern Louisiana during winters 2001 (filled bars) and 2002 (unfilled bars). Home-range size was not stable at nine locations, but our data showed that estimates at nine locations probably represented at least 74% of the actual home range for all individuals. Mean home-range size did not differ between study years, study sites, or burn treatments, as revealed by one-way ANOVAs.

ments ($F_{2,9} = 24.32$, $P < 0.001$; Fig. 3A). Year-0 sites had the lowest vegetation density close to the ground and the greatest vegetation height (Bonferroni, 0 versus 1, $P = 0.007$; 0 versus 2, $P < 0.001$; Table 3). Density increased and height decreased as time since burn increased. Individual study sites within burn treatment also differed from one another along the Height/Density axis ($F_{9,98} = 5.27$, $P < 0.001$). The amount of woody vegetation did not differ among burn treatments ($F_{2,9} = 0.91$, $P = 0.44$; Table 3), although sites within burn treatment had significantly different amounts of woody vegetation ($F_{9,98} = 3.98$, $P < 0.001$; Fig. 3A).

Grass species composition.—Among the nine dominant grass morphotypes (Table 2), seven loaded onto two orthogonal factors, explaining 53.1% of the variation in the data set. Principal components axis one (Species Diversity) showed high positive loadings for *Dichanthelium scabriusculum*, *Panicum virgatum/P. rigidulum*, and *Andropogon* spp./*Schizachyrium scoparium*. *Muhlenbergia expansa* without mature inflorescences and *Schizachyrium tenerum* had high negative loadings

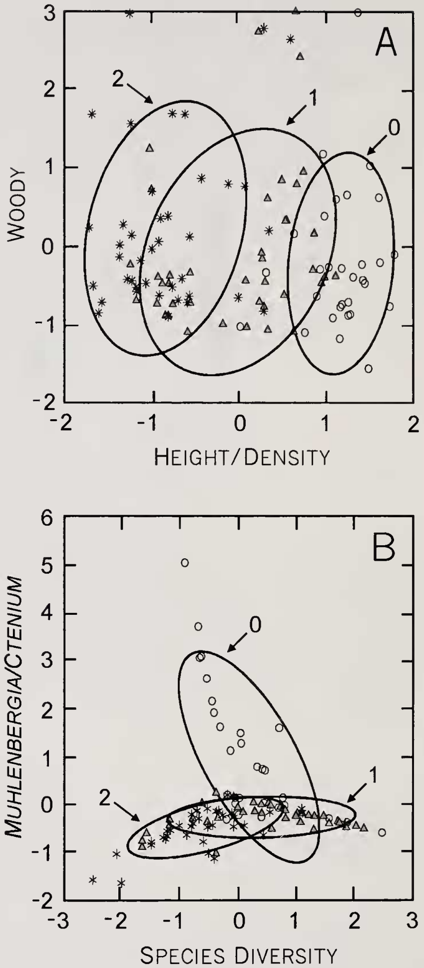

FIG. 3. Scatter plots of PCA scores for vegetation structure (A) and percent cover of dominant grass species (B) during winters 2001 and 2002 in southeastern Louisiana pine savannas. Each symbol represents a vegetation plot. Plots are grouped by burn treatment (0, 1, and 2 years since last burn), with ellipses delineating one standard deviation from the burn-treatment means. Circles represent plots in the year-0 burn treatment, triangles represent year 1, and asterisks represent year 2. (A) Burn treatments differ in height and density, but not in amount of woody vegetation. On the Height/Density axis, year-0 sites had the tallest vegetation and the lowest vegetation density near the ground. On the Woody axis, burn treatments did not differ in amount of woody vegetation. (B) Species diversity was slightly higher in the year-1 burn treatment than in the year-2 treatment. Sites in the year-0 burn treatment had significantly greater densities of *Muhlenbergia expansa* with mature inflorescences and *Ctenium aromaticum* than sites in the year-2 treatment.

TABLE 3. Mean vegetation measurements for southeastern Louisiana pine savannas in three burn treatment classes. Sites were either 0, 1, or 2 years since last burn, as sampled during the winters of 2001 and 2002. We used these variables, except seed abundance, which was considered separately, to create principal components factors representing vegetation structure and dominant grass species composition. Nested ANOVA revealed differences in vegetation structure, dominant grass species composition, and seed abundance among burn treatments.

	Year 0		Year 1		Year 2	
Variable	Mean	SE	Mean	SE	Mean	SE
Vegetation structure						
Height (m)	1.28	0.02	1.21	0.03	0.98	0.02
Density 0–0.1 m (no. of contacts)	3.31	0.24	6.55	0.31	8.08	0.28
Density 0.1–0.2 m (no. of contacts)	2.38	0.18	5.18	0.32	6.50	0.28
Density 0.2–0.3 m (no. of contacts)	1.37	0.15	2.95	0.23	3.88	0.18
Number of trees >7.5 cm dbh	1.93	0.41	2.00	0.53	2.39	0.58
Percent shrub cover	23.50	2.91	26.02	2.73	31.35	3.30
Number of woody hits	2.13	0.43	1.57	0.41	1.73	0.28
Percent cover of dominant grass species						
Andropogon spp./*Schizachyrium scoparium*	21.33	2.47	16.50	2.07	18.00	2.39
Panicum virgatum/P. rigidulum	5.17	1.72	8.75	1.46	2.13	0.91
Dichanthelium scabriusculum	5.67	1.72	16.13	2.81	6.13	1.92
Schizachyrium tenerum	2.17	1.12	11.25	3.53	15.88	3.31
Muhlenbergia expansa	11.67	2.83	0.13	0.13	0.88	0.87
Muhlenbergia expansa (without mature inflorescences)	0.67	0.67	5.75	1.39	26.88	3.20
Ctenium aromaticum	8.67	3.06	0.00	0.00	0.00	0.00
Aristida spp.	3.17	1.00	6.88	1.35	11.13	2.61
Dichanthelium spp.	2.50	1.45	20.88	4.24	26.63	4.16
Seed density						
Number of stalks/m^2 with mature inflorescences	83.61	7.91	52.24	7.59	23.45	4.57

on this axis. High positive loadings indicate high species diversity and high negative loadings indicate low species diversity. Vegetation plots that load positively on this axis have a high proportion of a number of dominant species, while plots loading negatively are covered by just one or two dominant species. Principal components axis two (*MUHLENBERGIA/CTENIUM*) was characterized by high loadings of *Muhlenbergia expansa* with mature inflorescences and *Ctenium aromaticum* and explained 25.3% of the variation in the data. *Aristida* spp. and *Dichanthelium* spp. without mature inflorescences did not load onto either factor and are included separately in the multiple regression analysis described below.

Burn treatments were marginally distinct from one another along the SPECIES DIVERSITY axis ($F_{2,9} = 3.20$, $P = 0.10$; Fig. 3B). Year-2 sites loaded negatively on this axis and tended to be less diverse than sites in burn treatments 0 and 1. Year-2 sites were dominated by *Muhlenbergia expansa* with no mature inflorescences and/or *Schizachyrium tenerum* (Table 3). Year-1 sites had positive loadings on this axis. These sites had high percent covers of *Dichanthelium scabriusculum, Panicum virgatum/P. rigidulum, and Andropogon* spp./*Schizachyrium scoparium* and tended to have the highest diversity of grasses (Table 3). Year-0 sites were better described by principle components axis two (*MUHLENBERGIA/CTENIUM*, see below). Sites within burn treatment levels differed significantly from one another along the SPECIES DIVERSITY axis ($F_{9,97} = 6.78$, $P < 0.001$).

The *MUHLENBERGIA/CTENIUM* principal components axis separated year-0 sites from year-2 sites ($F_{2,9} = 5.70$, $P = 0.025$; Bonferroni, $P = 0.025$; Fig. 3B). Year-0 sites loaded high and positive on this axis and had a greater abundance of *Muhlenbergia expansa* with mature inflorescences and *Ctenium aromaticum* than year-2 sites (Table 3). Sites within burn treatment differed from one another in abundance of *Muhlenbergia* with mature inflorescences and *Ctenium* ($F_{9,97} = 5.75$, $P < 0.001$).

Seed abundance.—The number of stalks

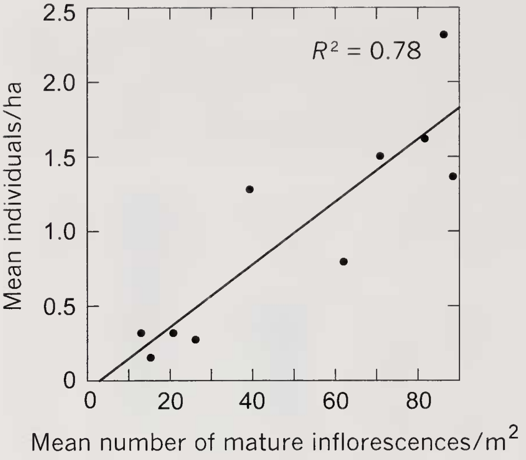

FIG. 4. Mean number of mature inflorescences/m^2 is the best predictor of Henslow's Sparrow abundance in southeastern Louisiana pine savannas during winters 2001 and 2002, as revealed by a backwards-stepping multiple linear regression relating habitat characteristics to Henslow's Sparrow abundance.

with mature inflorescences differed among burn treatments ($F_{2,8}$ = 13.91, P = 0.002; Table 3). Seeds were more abundant at year-0 and year-1 sites than at year-2 sites (Bonferroni, 0 versus 1: P = 0.17; 0 versus 2: P = 0.002; 1 versus 2: P = 0.061; Table 3). Seed abundance also varied among study sites within burn treatment ($F_{8,86}$ = 2.15, P = 0.039), but it did not vary across study years ($F_{1,105}$ = 0.82, P = 0.37). We removed three outliers with higher than expected seed abundances for their study site (Studentized residual >7.0).

Relationship of Henslow's Sparrow abundance to vegetation characteristics.—We used vegetation structure and species composition PCA scores, ranked percent cover values for *Aristida* spp. and *Dichanthelium* spp., and values for seed abundance in a backwards-stepwise multiple regression analysis to examine the relationship between Henslow's Sparrow abundance and vegetation characteristics. Mean seed abundance was the best predictor of Henslow's Sparrow relative abundance ($F_{1,8}$ = 27.74, P = 0.001, R^2 = 0.78; Fig. 4). HEIGHT/DENSITY scores were significantly correlated with mean seed abundance values (r = 0.93, P = 0.003). HEIGHT/DENSITY scores were also highly, but not significantly, correlated with Henslow's Sparrow abundance (r = 0.78, P = 0.20). *MUHLENBERGIA/CTENIUM*, SPECIES DIVERSITY, and WOODY scores did not explain a significant amount of the variation in Henslow's Sparrow abundance, nor did the percent cover of two grass species that did not load onto the PCA, *Aristida* spp. and *Dichanthelium* spp.

DISCUSSION

The clear message from this and other studies is that Henslow's Sparrows use winter habitat with a recent history of disturbance. At our study sites, we saw the highest numbers of Henslow's Sparrows in longleaf pine savanna that was burned the previous growing season. Relative abundance of Henslow's Sparrows decreased with increasing time since burn. We found significant differences in relative abundance among individual study sites of the same burn age, but most sites changed predictably between years. Across sites, mean abundance decreased by over 90% between sites burned the previous growing season and those not burned for 3 years. Radio-tagged individuals maintained small, stable home ranges over the study period, but home-range size was not related to abundance or burn treatment. We also found evidence of between-year site fidelity.

As in our study, studies of Henslow's Sparrows inhabiting lowland pitcher plant bogs and upland savanna managed for timber production revealed an inverse relationship between abundance and time since burn (Carrie et al. 2002, Tucker and Robinson 2003). Mechanical disturbance may have the same effect as burning, at least on some clearcut pine plantations (Plentovich et al. 1999). It is unknown to what extent Henslow's Sparrows use other grasslands that experience periodic burning or mowing, such as power line right-of-ways and agricultural grasslands. Preliminary investigations have found Henslow's Sparrows wintering along power line right-of-ways (Burhans 2002; CLB unpubl. data). The restricted movement patterns of wintering Henslow's Sparrows may allow them to exploit these long, thin strips of habitat. Winter use of agricultural lands needs to be investigated, but land-use practices, such as midwinter haying, may have a negative effect on winter populations.

We used a novel mist-net sampling technique that proved to be an effective means of capturing, banding, and estimating the abundance of Henslow's Sparrows. We evaluated the technique by observing the behavior of 10 radio-tagged individuals during sampling events. All radio-tagged birds flew above and landed back into the herbaceous layer when approached by the sampling team, suggesting that individuals exhibit a predictable response when approached. There was no relationship between team size and relative abundance of Henslow's Sparrows, suggesting that variations in team size did not affect abundance estimates. Within seasons, we expected to recapture more than 8 of the 88 individuals banded; this low recapture rate suggests that individuals may learn net avoidance in subsequent sampling periods. We do not know whether differences in detectability among treatments may have influenced our results, but this could be examined with additional recapture data.

Our recapture and telemetry data confirm that Henslow's Sparrows exhibit within-season site fidelity (see also Plentovich et al. 1998). All within-year recaptures occurred within the 6.25-ha site of original capture, and recapture data showed that Henslow's Sparrows could use the same habitat patch for up to 70 days. Two individuals were recaptured between study years. Both recaptures occurred within the management area of original capture, including one within the same study site, which could suggest some local between-year site fidelity for wintering Henslow's Sparrows. The individual that returned to the same study site returned as the site transitioned to a year-2 burn treatment. This site (LRS) had a higher relative abundance of Henslow's Sparrows than any other site in the year-2 burn treatment, suggesting that this site was somehow more suitable for wintering Henslow's Sparrows, independent of burn treatment. The other returning individual exhibited a habitat use pattern predicted by our sampling results, moving from a site in burn treatment 1 (LRS), to a site 1.16 km away, burned the previous growing season (RAM). Plentovich et al. (1998) found that Henslow's Sparrows exhibited site fidelity over one season and speculated that the absence of between-year recaptures indicated that preferred winter site conditions were too ephemeral—compared to an individual's life span—to encourage between-year site fidelity. While this seems likely, our two between-year recaptures indicated that some, possibly regional, form of between-year site fidelity may exist and that, depending on local conditions, habitat patches may remain suitable in consecutive seasons. Still, radio-tracking data and within-year recaptures suggest that arriving individuals must be able to select a habitat patch that will be suitable for the entire season. Examining settlement patterns and age-structure of wintering Henslow's Sparrows across a range of habitat patches may reveal more about how this process occurs.

Radio-tagged Henslow's Sparrows maintained stable home ranges over the winter. Radio-tagged individuals were consistently located in the same area of a study site over the sampling period. Our estimates of home-range size must be considered minimum estimates, as home-range size did not stabilize for any radio-tagged individual over the sampling period. Even so, our home-range size estimate (0.30 ha) roughly agrees with a simultaneous study of wintering Henslow's Sparrows at the Mississippi Sandhill Crane Refuge. In Mississippi, the mean home-range size (minimum convex polygon, 95% kernel) was 0.45 ha ($n = 42$ individuals with at least 21 locations; Thatcher 2003).

Home-range size did not differ among burn treatments or across study years. Furthermore, home-range size did not show any relationship to relative abundance, a surprising observation, considering that home-range/abundance relationships are widely documented in the literature (Wiens 1973, Smith and Shugart 1987, Wunderle 1995, Haggerty 1998, Brown et al. 2000). Perhaps Henslow's Sparrows have partially overlapping, non-defended home ranges during winter, since abundance relationships usually occur when species maintain exclusive territories. Other investigators of wintering *Ammodramus* sparrows have observed a distinctive pattern of use of space in these species (Gryzbowski 1983, Gordon 2000). Small, weak-flying species with cryptic coloration are often solitary and evenly distributed across their habitat during winter (Pulliam and Mills 1977, Gryzbowski 1983). Gryzbowski (1983) suggested that this behavior may allow solitary species to exploit areas with less abundant seed resources. These species' predator avoidance and resource acquisition strategies differ from those of gregarious, flocking species, which exhibit large-scale movements to exploit patches of resource-rich habitat (Grzybowski 1983, Gordon 2000).

It has been suggested that wintering Henslow's Sparrows may not require the large areas of grassland habitat essential to breeding populations (Herkert 1991, Burhans 2002). In lowland pitcher plant bogs, Tucker and Robinson (2003) found Henslow's Sparrows wintering in habitat patches as small as 0.06 ha. We did not test for the effects of area, but the differences in mean size of study sites among studies of wintering Henslow's Sparrows may be revealing. Our study sites were considerably larger than the majority of sites in previous studies (mean = 5.9 ha versus 0.2–1.0 ha) and all of our study sites were located within a larger matrix of savanna that had been burned within the last several years. Whereas Tucker and Robinson (2003) found that abundance of wintering Henslow's Sparrows increased with area, density was not related to bog area. This result could indicate that Henslow's Sparrows will use suitable habitat patches of any size, or it could reflect the fact that the majority of patches examined were very small (only 2 of 47 sites were >1.0 ha). Further investigations of settlement patterns and individual home-range overlap could shed more light on winter area requirements.

As in previous studies, we found that habitat characteristics varied across burn treatments and certain characteristics were correlated with relative abundance of Henslow's Sparrows. Vegetation structure, dominant grass species composition, and seed abundance varied across burn treatments. Sites burned the previous growing season had lower vegetation density within 0.3 m of the ground and greater vegetation height than sites burned 1 or 2 years prior to the previous growing season. Sites burned the previous growing season also had higher percent cover of *Muhlenbergia expansa* and *Ctenium aromaticum* and higher seed abundance than sites burned 2 years prior to the previous growing season. Sites burned 1 year before sampling had the highest species diversity of dominant grasses. We were surprised that the amount of woody vegetation did not vary across burn treatments, but this could be a reflection of our site-selection criterion of minimal shrub cover.

Seed abundance stood out as the best predictor of Henslow's Sparrow relative abundance. A high percent frequency of seeds was also one of the most important predictors of Henslow's Sparrow occupancy of pitcher plant bogs along the Alabama/Florida border (Tucker and Robinson 2003). Similarly, on clearcut pine plantations in Alabama, one of the best predictors was the presence of *Panicum verrucosum* (Plentovich et al. 1999), a prolific seed producer that is common after soil disturbance. Like other *Ammodramus* species, Henslow's Sparrows probably rely mostly on seeds for their winter diet (Grzybowski 1983; M. S. Woodrey unpubl. data), although which seed species play the most important role in winter diet is unknown. Preliminary data indicate that *Muhlenbergia expansa*, *Dichanthelium* spp., *Rhynchospora* spp., and *Eupatorium* spp. may be important elements in the winter diet of Henslow's Sparrows (J. K. DiMiceli pers. comm.). Future studies should avoid overlooking inconspicuous species that could be important seed resources. For example, *Rhynchospora* spp. are a suite of species with diverse growth habits; some *Rhynchospora* produce tiny seeds and grow only a few centimeters tall. We observed these species forming a layer under taller grasses on some of our study sites, but did not include them in our measurements of species composition or seed abundance. These preliminary observations stress the importance of considering seed abundance and species composition at a fine scale.

After seed abundance, vegetation structure was the next most important predictor of Henslow's Sparrow abundance. Sites with vegetation heights >1.0 m and low vegetation density <0.3 m consistently had the greatest numbers of wintering Henslow's Sparrows. Carrie et al. (2002) also found that herbaceous cover and low vegetation density near the ground were important factors in discriminating between occupied and unoccupied sites. Tall vegetation may impede detection by predators, whereas low vegetation density near the ground may facilitate foraging movements for this weak-flying species.

Our habitat association results are supported by previous studies, although direct comparisons can be problematic. In two of the three previous studies, the second most important predictor of Henslow's Sparrow presence was high vegetation density at or below 1.0 m (Plentovich et al. 1999, Tucker and Robinson 2003); in our study, Henslow's Sparrow abundance was correlated with what is seemingly the exact opposite, low vegetation density near the ground. This apparent contradiction could have two sources. First, the relative difference in vegetation structure among our study sites is probably lower than in previous studies. We studied eight sites, located within continuous savanna habitat and dominated by native herbaceous species; the majority of our study sites were occupied by Henslow's Sparrows. Other studies examined a greater number of study sites representing a broader range of habitat structures and birds were absent from many of these sites. Second, the manner in which some studies quantified vegetation structure makes it difficult to separate vegetation density from vegetation height. In those studies, vegetation density was measured as the number of 10-cm increments where a certain type of vegetation was present (Plentovich et al. 1999, Tucker and Robinson 2003). Using this measure, sites with high vegetation density will also have taller vegetation, while not necessarily having high vegetation density near the ground. For example, on clearcut pine plantations (Plentovich et al. 1999) and lowland pitcher plant bogs (Tucker and Robinson 2003), Henslow's Sparrow presence/abundance was correlated with high densities of herbaceous cover. These results may correspond to our conclusion that abundance is greater on sites with taller vegetation, rather than contradict our vegetation density findings. Looking beyond these study-site and data-collection differences, studies of wintering Henslow's Sparrows seem to agree that tall vegetation, low vegetation density near the ground, and high seed abundance are positively correlated with presence or abundance of Henslow's Sparrows (Plentovich et al. 1999, Carrie et al. 2002, Tucker and Robinson 2003).

Management implications.—The absence of a natural disturbance regime on the southeastern Gulf Coastal Plain makes active management essential to wintering populations of Henslow's Sparrows. Habitat patches burned the previous growing season, with vegetation >1.0-m tall, low vegetation density near the ground, and high seed abundance had the greatest relative abundance of Henslow's Sparrows across our study sites. Many herbaceous savanna species require a fire to flower, and species that follow fire often decrease in abundance as litter accumulates (Lemon 1949, Walker 1993). However, some herbaceous species are good competitors in the presence of litter, only reaching significant densities a few seasons after a burn, and fire interval may be important in maintaining seed bank diversity (Lemon 1949, Hodgkins 1958). Litter accumulation is also important in generating the high temperatures needed by some species to flower (Komarek 1965); burning too frequently can lead to a thin herbaceous layer, made up of a few fire-following species. Our relative abundance estimates demonstrate that a 10-ha area of savanna burned the previous growing season will support about 25 sparrows. After 1 year, the number will drop to around 10 individuals. Two years after a fire, the habitat will support approximately 1 individual/10 ha. If remnants of longleaf pine savanna and other similar grassland habitats are to support significant numbers of wintering Henslow's Sparrows, we recommend a biennial, rotating burn schedule. Future studies examining landscape-scale fire regimes, winter settlement patterns, predation risk, and diet are essential and will lead to a further refinement of these management recommendations.

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